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The Distribution Centers of the Melanoplina (Orthoptera; Acrididae; Cyrtacanthacridinae)

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Since the days of Eduard Suess it has been orthodox to ascribe to an Angaran center the role of a *locus communis* for an overwhelming percentage of the elements of the Holarctic biota. While in many cases this may, and probably does, provide an explanation of what has taken place, in others, where it has been assumed to be a basic postulate which perforce must be accepted, this theory can have value only if it is supported by the weight of known evidence.

In vertebrate paleontology this type of evidence is now so increasingly comprehensive that those who consider faunistic histories or movements in any group, must acquaint themselves with at least some of the broad conclusions which have been drawn, particularly in the past few decades, from the steadily augmenting amount of mammalian evidence. While it has long seemed fashionable to ascribe a very secondary role to the Nearctic region as a biotic evolutionary center, and to credit the Palearctic with a markedly predominating one in the evolution of the Holarctic biota, this latter is occasionally refuted by fossil evidence. The migrations of whole groups of mammals, or their regional extinction, are, as with the camels and tapirs, sometimes made clearly evident by this record. Admittedly this mammalian evidence is almost entirely Caenozoic in coverage, and in considerable part late Caenozoic, but many tribes of insects are probably no older, and it is important for all ento-

mologists who discuss faunal histories to consider what fellow-workers have ascertained in regard to other animals. Also, when we have little or no fossil evidence for the group from which to reason, we must turn to our knowledge of the existing fauna, and see what we may learn from it.

To digress momentarily, however, in the constant stressing of the role of Angara in biotic history, little attention is given to that similarly ancient, and much larger, part of North America called Laurentia by geologists. To quote Suess himself:¹ "That vast region of North America which is formed of ancient rocks overlain by horizontal Cambrian sediments has received the name of Laurentia. It comprises the whole of the Canadian shield, but if we are to regard it as a tectonic unit, we must include the whole of the flat-bedded superstructure up to some natural boundary. Such a boundary is presented by the Rocky Mountains, the United States chain, and, for nearly their whole length, the Appalachians also. The Colorado plateau, a fragment of table land, bounded on the east by the southern branches of the Rocky Mountains, ought also, perhaps, be regarded as a part of Laurentia." Further (p. 257) he adds: "Laurentia extends from south Texas to the Arctic Ocean through 53 or 54 degrees of latitude, and from the mouth of the Mackenzie to the east coast of Greenland through more than 110 degrees of longitude. . . . Laurentia is a very ancient unit. *It behaves towards all the younger folds as a foreland* [his italics]."

Of the Nearctic acridid fauna the most numerous in species, and often so areally in individuals of different species as well, is the tribe to which the name Melanoplinae has warrantedly been applied.² Long known as the Podismae (or Podismini), from one of its Old World genera, which is also now found to have a single representative in the Nearctic Region (*P. hesperus* (Hebard)³), this assemblage has, in the Old World, components distributed over Eurasia from western Europe to China, Korea and Japan, and from subarctic districts to the mountains of

¹ "The Face of the Earth" (English translation of the classic "Das Antlitz der Erde"), IV, pp. 251 and 257.

² See ROBERTS, Proc. Acad. Nat. Sci. Phila., XCIX, p. 202 (1947).

³ See REHN and REHN, Trans. Amer. Entom. Soc., LXV, p. 88 (1939).

southern Europe, the Himalayas, Formosa and Tonkin. Within this great area it breaks up into a number of genera, although it is also unrepresented over extensive sections of the Palearctic Region, and apparently does not penetrate peninsular India, Burma or Indo-Malaya, and in Indo-China reaches only to Tonkin. All we know of the paleontological history of the tribe is that two existing species, representing two genera (*Miramella* and *Bohemanella*), occur in the Pleistocene of Starunia, in the Polish Carpathians.⁴

In the New World we find members of the Melanoplinae extending over a far greater extent of latitude than in the Old World, from the Arctic Circle to at least south-central Argentina and Chile, or well over one hundred degrees of latitude, reaching upwards to arctic alpine or paramo conditions in the Rocky Mountains, the Sierra Nevada, the great Mexican volcanoes, the main Andes, the Sierra Nevada de Santa Marta of Colombia and in the Venezuelan Andes. The sole area in the hemisphere, within these bounds, where they are unrepresented is the Amazonian lowland, an area where numerous other groups, elsewhere widely distributed in South America, are also absent. While as yet not critically studied and hence unreported the tribe is also represented by brachypterous material in my hands from mountain areas of certain of the Greater Antilles. This last fact, alone, is conclusive evidence that their arrival in Antillia was by no means recent. In North America members of the tribe are present virtually everywhere south of the Arctic barren grounds, even in the most extreme deserts and also under arctic alpine conditions, thus exhibiting in that part of the world an adaptability which predicates long association and adjustment, even where it has meant retreat and advance over the greatest area in the world now exposed which was subject to repeated Pleistocene glaciation. In passing it may be pointed out that no Palearctic member of the Podismini is known to occur in true deserts.

The distinguished French orthopterist Dr. Lucien Chopard, in

⁴ See ZEUNER, *Starunia*, 3, pp. 9-11 (1934); *Ann. and Mag. Nat. Hist.* (11) VIII, p. 513 (1941).

his classic work on the biology of the Orthoptera,⁵ dismisses the origin of *Melanoplus*, the dominant North American genus of the Melanoplini, with the following: "il semble certain que le premier [i.e., *Melanoplus*] est d'origine asiatique." In an earlier study⁶ Chopard had reached certain conclusions regarding the development of centers of speciation of that genus in the United States which, unfortunately, do not correctly interpret the evidence he was summarizing, this latter very largely drawn from the researches of certain contemporary American orthopterists, of whom the writer was quoted as one. This aspect of the subject will be commented upon elsewhere.

In the Old World we find the Melanoplini showing marked radiative or development centers in the following areas: (1) the Pyrenees and other mountains of Spain, the Alps, the Italian mountains, the Carpathians and the mountains of all of the Balkan Peninsula and Greece; (2) the Caucasus; (3) the Amur (or Ussuri) region of eastern Siberia, the mountains of China, Japan, Formosa and the Himalayas. Glaciation was undoubtedly a factor which made certain of these various component districts subsidiary evolutionary centers. While species occur in the intervening territories, the above mentioned units would appear to be the centers of marked diversity or most pronounced individuality of types. No member of the tribe occurs in the Palearctic portion of Africa or in Iran, while representation in Anatolia is very limited.

In the New World there are three comparable major evolutionary centers for the Melanoplini, between each of which are areas where the tribe is sparsely represented, but, as already stated, it is absent, within the overall encompassing boundaries, only from the markedly tropical lowlands of Amazonia. The first of these evolutionary centers covers Canada (with Alaska), the United States and Mexico north of the Isthmus of Tehuantepec. The second is in the Venezuelan Andes and adjacent,

⁵ "Le Biologie des Orthoptères." By LUCIEN CHOPARD. Paris. 1938. [Reference is made to page 14.]

⁶ "La faune des Orthoptères des montagnes des Etats Unis et ses rapports avec la faune palearctique." Société de Biogéographie. Paris. 1928. 8 pp.

chiefly montane, areas in northern and eastern Colombia. The third covers that portion of South America from approximately 15° south latitude southward to south-central Argentina and Chile, with certain elements reaching somewhat to the northward in the Peruvian and Ecuadorian Andes. But two genera bridge the gap in Central America, these being *Aidemona* and *Trigonophymus*, the former of which ranges from the southwestern United States to Colombia, while the latter is an intrusive type from its area of maximum development in southern South America. Our knowledge of the geological and hydrographic history of Central America makes reasonably clear why this break is present, and which *Aidemona*, clearly from the north, and *Trigonophymus*, as certainly from the south, have crossed possibly in late Caenozoic times. The geological history of northeastern Colombia and northwestern Venezuela is complex, and has been summarized by Schuchert.⁷ The relative antiquity of the tableland of eastern and central Brazil is well known, and its probable role as a radiative evolutionary center for the third, more austral, aggregation is a logical conclusion.

Analyzing the recognized generic components of the Melano-plini we find that 27 genera occur in Eurasia, of which one is regarded by Ramme as a synonym of another so included, and of these three, i.e., *Podisua*, *Zubovskya* and *Bohemanella*, are also present in the Nearctic, while from the Nearctic and the Neotropical together we know at present 59 genera, of which but three—above-mentioned—also occur in the Old World. Only *Aidemona*, *Trigonophymus* (but two species outside of the most southern center⁸) and *Propedies* (but one species outside the same area⁹) occur in more than one of the three radiative areas above outlined, and of these *Trigonophymus* is the sole one present in all three, and in the largest and most impor-

⁷ "Historical Geology of the Antillean-Caribbean Region." 1935. [Pages 624-695 treat of Colombia and Venezuela.]

⁸ *T. punctulatus* and *T. notatus*, the former reaching northward to Costa Rica, the latter solely Mexican.

⁹ *P. minutus* Roberts, from Curaçao. The latter island is regarded as part of the Coast Range or Caribbean Andes of northward Venezuela. See Schuchert, idem, p. 678.

tant of these it occurs only in the mountains of central and southern Mexico. Turning to the number of species and subspecies known, as a possible index to evolutionary complexity, and conservatively basing the count on those now regarded as valid by workers most familiar with the respective faunas, we find a maximum of 83 species or subspecies in the Palearctic Region, while the Nearctic and Neotropical representation comprises at least 471 species or subspecies.

In the Palearctic and impinging Oriental regions we find definite localization of most of the genera, with the largest numbers of these found in what may roughly be termed the Mediterranean-Alpine-Balkan montane center (6 genera), northeastern Asia with Korea and Japan (6), southeastern Asia (exclusive of the Himalayan subregion) (6) and the Himalayas and the Caucasus each with 2 (these endemics). Those of relatively broad distribution in the Palearctic are few (4), and, of these, two (*Podisma* and *Bohemanella*) are shared with the Nearctic. However, there is no single area in the Palearctic Region, even of great size, which could be regarded as the outstanding evolutionary center of the Melanoplinae, on the basis of number of genera or of species or subspecies there occurring at present. The greatest diversity specifically is found in the Mediterranean-Alpine-Balkan center, but the number of genera there represented is relatively low (vide supra).

In the New World 40 genera occur north of the Isthmus of Tehuantepec, this total exclusive of three shared with the Old World and two with areas to the southward; the Colombian-Venezuelan center has four genera plus *Propedies* which it shares with more austral America and *Aidemona* and *Trigonophymus* with more northern regions; while the Brazilian-Argentine center holds eight peculiar genera plus *Propedies* shared with the Colombian-Venezuelan one, and *Trigonophymus* with both of the other New World centers. Samplings of the number of genera present in representative areas of the North American-Mexican center alone give us the following figures: New Jersey and Pennsylvania 6, North Carolina 5, Florida 6, Montana 7, Colorado 8, Texas 13, Washington and Oregon 8,

California 7, Arizona 7. The number of individual genera involved in these sample tabulations (all within the United States alone) totals 32, or five more than all known from the entire sweep of Eurasia.

It is conceivable that genera such as *Podisma* and *Zubovskya* have entered the Nearctic from the Palearctic at a relatively recent period, and the same may be true of the Nearctic *Prumnacris*, *Buckellacris* and *Nisquallia*, while *Bohemanella*, the single component of which was long considered a *Melanoplus*, may have similarly crossed the Bering land-bridge but in the reverse direction (i.e., from the Nearctic). On the other hand *Zubovskya* was clearly in North America before the Pleistocene, as its present discontinuous distribution on that continent unquestionably points to glacial ice-sheets as the agency separating the eastern and western sections of its North American distribution.¹⁰ It is also within the realms of possibility that the eastern Asiatic forms of *Zubovskya* (all known from the Palearctic) are not the parent stock, but instead are intrusives from the New World, where the genus is present over a far greater area. Clearly *Bohemanella* has been derived from one of the montane lines of the genus *Melanoplus*, to which it is exceedingly close if actually distinct generically. None of the other very considerable representation of melanoploid genera in the New World shows any very close resemblance to Old World ones, and we are forced to the conclusion that their evolution has taken place in the New World, and that while migration and counter-migration may have taken, and probably did take, place the limited Old World representation certainly cannot be considered the parent stock, or that area the evolutionary center of the whole, in view of the disparity in the development of the tribe in these two great areas.

It is hardly conceivable that evolutionary centers such as that in the southern half of South America have developed in a relatively short period of time from a parent one as distant as east-central Asia (i.e., Angara), particularly where we consider the degree and extent in time of the isolation which tropical America

¹⁰ See REHN and REHN, Trans. Amer. Entom. Soc., LXII, p. 8 (1936).

(i.e., south of Tehuantepec) is known to have had.¹¹ Instead it seems much more logical and warranted to regard the Melanoplinae as a basic New World entity, probably developing rather early in North America, where by far its greatest complexity is found today, the South American centers being established subsequently during certain of the periods of connection with North America.¹² The isolation of the two South American centers from one another is understandable from the viewpoint of Andean orogeny and the development of the great Amazon basin as a barrier to certain forms of life. The presence in North America of genera not widely removed from some of those of the Palearctic Region can as well be interpreted through a westward movement of their progenitors as the usual assumption that the reverse was true. This we know from fossil evidence has taken place in a number of the higher forms of animal life.

To summarize, in the New World we have 59 genera and, conservatively evaluated, 471 species and subspecies of the Melanoplinae, these found over a great range of latitude and including almost all possible conditions, or from above the Arctic Circle to about 41° south latitude, and from below sea-level (in parts of California) to arctic alpine summits sometimes bordering perpetual snow (in Washington and Oregon), and from the Atlantic to the Pacific coasts. Three major centers of New World radiative evolution are evident, the separation of which is due to their geological backgrounds. The absence of members of the Melanoplinae from areas of the Palearctic, such as North Africa, Iran and much of Anatolia, would indicate that the tribe was not present when these areas received most of their other orthopteran elements of undoubted Palearctic origin. The fact that many, in fact most, of the Palearctic Melanoplinae are montane does not militate against this argument, as montane areas

¹¹ Except for Lower Oligocene times this isolation is regarded by Schuchert as having been continuous from the Upper Eocene to at least the Lower Pliocene. See SCHUCHERT, "Historical Geology of the Antillean-Caribbean Region," maps 10 to 16.

¹² For a careful and critical analysis of this latter question in its Caenozoic aspect the reader is referred to SIMPSON, G. G., 1950, "History of the Fauna of Latin America," *American Scientist*, XXXVIII, pp. 361-389, 10 figs.

are, and long have been, definite features of the apparent regional centers of the Old World, and in the Palearctic regions mentioned where the Melanoplinae are absent purely montane species represent other groups of insects. On the other hand in the Nearctic they apparently occupied, and still occupy, almost every type of environment, persisted through the sweeping Pleistocene glaciations, and there developed into one of the most highly diversified existing tribes of the Acridoidea. To disregard the evidence of an existing fauna of remarkable complexity—clearly not a development of a short period of time—is hardly justifiable today. Much of the manner of thought which failed to grasp the obvious conclusion here reached, has been due to an absence of first-hand acquaintance with the elements of some of the faunas involved, and a lack of knowledge of the very broad adaptability to almost all types of environments found in many of the Nearctic Melanoplinae. A personal comprehension of the field conditions under which all but two of the Nearctic genera live has enabled me to approach this problem with an open mind. It has been my privilege to study either in the field or in the laboratory, or in both, all the genera and all but a very limited number of the species or subspecies of Nearctic and Neotropical Melanoplinae, and as laboratory material all but a few of the genera and the majority of the species of the same known from Eurasia.

A New Milliped of the Genus *Cylindrodesmus* from Palmyra Island

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In a small but interesting collection of chilopods and diplopods collected in Hawaiian and other Pacific islands were specimens of a new species of the genus *Cylindrodesmus* taken on Palmyra Id. in 1948. These and the other specimens of the collection were made by N. L. H. Krauss, through whose courtesy I have been privileged to study the material. The species here described makes the third to become known in *Cylindrodesmus*, the others being *C. hirsutus* Poc., the genero-